Culture Extends the Scope of Evolutionary Biology in the Great Apes

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Discoveries about the cultures and cultural capacities of the great apes have played a leading role in the recognition emerging in recent decades that cultural inheritance can be a significant factor in the lives not only of humans, but of non-human animals. This prominence derives in part from the fact that these primates are those with whom we share the most recent common ancestry, thus offering clues to the origins of our own thoroughgoing reliance on cumulative cultural achievements. In addition, the intense research focus on these species has spawned an unprecedented diversity of complementary methodological approaches, the results of which suggest that cultural phenomena pervade the lives of these apes, with potentially major implications for their broader evolutionary biology. Here I review what this extremely broad array of observational and experimental methodologies has taught us about the cultural lives of chimpanzees, gorillas and orangutans, and consider the ways in which this extends our wider understanding of primate biology and the processes of adaptation and evolution that shape it. I address these issues by first evaluating the extent to which the results of cultural inheritance echo a suite of core principles that underlie organic, Darwinian evolution, but also extend them in new ways; and secondly by assessing the principal causal interactions between the primary, genetically-based organic processes of evolution, and the secondary system of cultural inheritance that is based on social learning from others.

Social learning | culture | evolutionary biology | chimpanzee | gorilla | orangutan

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Recent decades have revealed social learning (learning from others) to be pervasive across the animal kingdom, with important implications for evolutionary biology at large (1), the subject of the Sackler Colloquium published here (2). The present article focuses on great apes: chimpanzee (*Pan troglodytes*), gorilla (*Gorilla gorilla*) and orangutan (*Pongo pygmaeus*). Other primates are dealt with elsewhere in the issue (3, 4). Despite an early report (5) we still know little about cultural phenomena in chimpanzees' rarer sister species, the bonobo (*Pan paniscus*) so bonobos are omitted here. I also make only limited reference to human culture, despite the fact we are technically also 'great apes'. Human culture is extensively treated in other papers in the issue.

I first survey the nature and scope of social learning and associated aspects of cultural transmission in great apes, concluding that the depth and diversity of observational and experimental evidence for cultural phenomena is unparalleled amongst non-human species. The evidence thus accumulated suggests that culture permeates the lives of the great apes in the breadth of behavioral repertoires affected, and also in their time-depth. This makes them evolutionarily significant. The authors of a comprehensive recent review of cetacean culture concluded that "Culture … is a major part of what the whales are" (6, p. 7; and see 7). Such a statement is obviously true for our own species (8-11); here I examine the justifications for thinking the phrase also has validity for great apes.

Following a sister review ranging much more widely across both vertebrates and invertebrates (1), I take eight core principles of evolution illuminated by Darwin (12) and assess the extent to which they apply to cultural phenomena in the great apes (henceforth simply 'apes'), as they do in humans (13). I then explore ways in which cultural inheritance goes yet further beyond these principles, creating new evolutionary phenomena. Finally I address interactions between the primary manifestations of organic evolution based on genetic inheritance, and the 'second inheritance system' (14) based on social learning. In a now long-standing human literature this has been called 'gene-culture co-evolution' (15), the logic of which (10, 16) should apply to other cultural animals (1, 7).

Diverse and Convergent Evidence for the Scope of Great Ape Culture

Geographic variation in traditions in the wild. In 1986 Goodall began to chart differences behavior patterns between chimpanzee study sites across Africa (17), proposing these as cultural variants where no genetic or environmental explanation was apparent (later called the 'method of exclusion'). The approach became more comprehensive with time (18, 19), eventually benefitting from a systematic collaboration between multiple long-term research groups (20, 21). The same was soon achieved by orangutan field researchers (22) and more recently by a gorilla consortium (23). These analyses converged in reporting multiple cultural variants in all three genera: 39 (*Pan*); 24 (*Pongo*) and 23 (*Gorilla*). These spanned apes' behavioral repertoires, including a great variety of tool use, food processing and social behavior, discussed further below. Further variants have continued to be intermittently reported for *Pan* (24) and *Pongo*, in the latter case leading to a revised tally of between 26-35 variants depending upon the criteria applied (25).

These surveys are vulnerable to false positives (it can be difficult to be sure that all alternatives to social learning have been excluded), and also false negatives (cultural adaptations to local environmental properties may be inappropriately excluded) (26). However, these pioneering efforts provided essential platforms for more refined approaches, some incorporating both genetic and environmental variables into analyses (27). Other advances yielded confirmatory evidence for culture through (i) more focused micro-habitat analyses for specific behaviors such as ant-dipping (28, 29); (ii) comparisons between neighboring communities sharing genes and habitat properties (30); and (iii) social learning experiments, as for nut-cracking (31-32)..

The broad geographic surveys thus provide an initially imperfect but progressively refined overall picture of ape cultural repertoires. The approach has been systematically applied to spider monkeys (*Ateles*, reporting 23 cultural variants) (33) but to my knowledge, not yet to other animals. Evidence exists for multiple cultural variants in other species such as killer whales, that display very different hunting repertoires (e.g. for fish versus seals), song repertoires and migratory patterns (6), but systematic tabulations have yet to facilitate direct cross-species comparisons.

Inter-group variation in traditions in captive communities. A parallel approach has compared neighboring communities in captive contexts, with the advantage that genetic and environmental explanations for group differences can be dismissed more cleanly. For example in the Chimpfunshi chimpanzee sanctuary in Zambia, a bizarre habit of inserting a blade of grass into one ear and leaving it there spread in one group but not in others (34). Moreover a distinctive 'hand-clasp' form of grooming was absent in this group and one other, yet customary in others where it additionally took different forms (35). Similar group contrasts were found in hard-shelled Strychnos fruits were opened (36), whilst at the Yerkes Center in the USA a further contrast in hand-clasp grooming emerged and spread over several years, remaining absent in another (37). These results reinforce those derived from the studies in the wild, outlined above.

Quantitative Evidence for Vertical, Mother to Offspring Transmission. A study of the ontogeny of using stem-tools for termite-fishing found that juvenile female chimpanzees spent significantly more time attending to their mother's fishing than did their male peers (38). Consistent with the skill being learned by observation, the young females tended to master the technique a whole year ahead of the males, with a significant tendency to match even the length of probe their mother typically inserted into the mound (38).

Researchers studying orangutans have called the focused visual attention of juveniles 'peering' (39) (see Fig.1). Building on studies documenting correlations between maternal and juvenile foraging profiles (40, 41), a suite of predictions were confirmed consistent with peering functioning to facilitate learning key survival skills (39). In foraging and nest-building contexts where peering is most frequent, it was found that (i) the frequency of peering in foraging contexts was predicted by the quantified complexity of processing operations and also by the skill's rarity; (ii) peering was followed by a higher rate of exploration of the item concerned, also confirmed specifically for the use of sticks in foraging, seen only at one of the two sites studied; (iii) peering rose along with the learning of new skills and diminished as competence was achieved; (iv) peering at nest-building was followed by a rise in nest-building over the next hour; (iv) developmentally, peering tracked the peak time of learning to make nests; and (v) by about age five, peering tipped below 50% directed at a juvenile's

mother and more towards others, from whom there was yet something to learn (39). Such observations offer a compelling case that juvenile apes' close peering facilitates learning major life skills.

< insert Fig. 1 about here >

Quantitative Evidence for Horizontal Transmission. There is both intra-community and inter-community evidence for horizontal transmission in the wild. An example of the former was tracked by network-based diffusion analysis, confirming that a novel chimpanzee behavior, using moss as water-sponge, spread from the alpha male along lines of social affiliation, providing quantitative circumstantial evidence for transmission (42). Examples of inter-community transmission include (i) a significant acceleration in habituation to human observers in a chimpanzee community being newly habituated, after two females immigrated from a well habituated community (43); and (ii) ant-fishing spread to a new community after the immigration of a proficient individual from a neighboring community where fishing was habitual (44).

Quantitative and Qualitative Evidence for Investment in Transmission. Video of termite fishing has documented skilled chimpanzee mothers donating tools to less competent juveniles (Supplementary Fig. S1), thence suffering a diminished duration and rate of termiting, whereas the recipient enjoyed improved fishing (45). The authors propose this meets commonly accepted criteria for a functional (as opposed to intentional) concept of 'teaching'. They also document mothers orally splitting their tool lengthwise to neatly make two functional tools, or bringing multiple tools, suggesting this partially buffers mothers from the costs of youngsters' demands. Alternatively it might be argued that these actions are essentially unnecessary and so represents the more compelling evidence the behavior has costs and therefore counts as teaching, even if not as active as teaching by scorpion provision in meerkats (46) or beaching to catch seals in killer whales (6). However, the pattern of costs and benefits suggests that this support has positive fitness benefits to the young, and parallel reports concerning use of tools for nutcracking have also been described (47).

An earlier report described more active involvement in curbing youngsters' exploration of potentially dangerous food-types. Haraiwa-Hasegawa (48, p. 280) reported that when an infant PN reached to touch some fig leaves, "her mother, FT, took PN's hand and moved it away from the leaves. As PN continued … FT took the leaves from PN's hand, plucked all the leaves within her arm's reach and dropped them to the ground." At least one other mother behaved similarly and "prohibited their infants only from feeding on the individual trees that they themselves never fed on".

Dyadic Experimental Studies of Social Learning. Experimental reports of social learning by naïve individuals from proficient models have multiplied for over a century in all great ape genera, tabulated and enumerated in successive reviews (49: n = 19 studies; 50: n = 33 further studies; 51: n = 25 studies comparing two or more ape species). The more recent experiments often adopt a highly informative 'two-action' approach, in which participants see either of two models, each trained to tackle a problem like opening a foraging box in a different way. Ideally a third, no-model control group is included. This method has demonstrated social learning in captive chimpanzees (52), gorillas (53) and orangutans (54), that implies the copying of whichever of the two actions (imitation) or movements of the manipulanda (emulation) were seen, rather than simpler processes of mere enhancement of the manipulanda (55). These approaches have further dissected the particular social learning processes at work, a topic beyond the scope of this review (see 56-59 for in-depth treatment). More relevant to present concerns and reviewed further below are extensions to these approaches to track successive cultural transmissions necessary to sustain traditions.

Nevertheless these dyadic experiments can importantly complement results from the field. For example, nut-cracking with natural hammer materials, found naturally only in West Africa (Fig. 2) is shown not explicable as an instinct in the West that is simply absent in the East, for East African chimpanzees exposed to proficient models became proficient, unlike controls in a no-model control condition, showing the behavior is (socially) learned (31, 32) (Fig. 2).

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Cultural Diffusion Experiments. Experiments focused on the broader phenomenon of cultural diffusion typically begin with models displaying different solutions to a task and then track their potential spread in others who witness them. Alternative variants provide important complementary information (63, 64). For example, the 'transmission chain' design pairs a first model (A) with a naïve individual (B), then when B achieves some competence criterion, they become a model for a further individual, and so on (B-C, C-D etc.). Achieving such configurations peacefully with apes requires sensitive experimental manouevering, but transmission has been demonstrated along chains of up to five participants in chimpanzees (65) and orangutans (66), as in children (65). This provides important models of transmission across cultural 'generations', implying a potential for cultural transmission across what would naturally be decades of ape life.

By contrast, 'open diffusion' designs mimic transmission in the wild where whole groups are exposed to alternative models; it is 'open' who watches and copies (or not). This design has been applied in chimpanzees and children in several experiments (67-69), including two where tool-use behavioral variants were transmitted across three groups with significant fidelity (69). This is important for interpreting putative cultures in the wild, such as the nut-cracking distributed across several hundred kilometers of West Africa, that would have required repeated inter-community transmission.

How Pervasive is the Role of Cultural Inheritance in the Lives of Great Apes?

Social Learning Shapes a Broad Repertoire of Cultural Variants. We can first examine this question by surveying the range of behaviors described in the cross-site comparisons summarized above (20-23, 27).

The chimpanzee lists of 1999-2001 include 30 different kinds of tool use ascribed to culture, all suggesting functional and adaptive payoffs beneficial to the performer's biological fitness (14, 21, 24). Others have been reported since, including sticks bitten and thus sometimes made sharp, used to stab or evict bushbaby prey at Fongoli in Senegal (70, 71) and a kit of stout tools to make tunnels, plus fine stems to fish down these and extract termites from nests deep underground (72). A majority of such tools are used in food extraction, but others are used in 'hygienic' actions like wiping blood or semen off fur, in protective 'comfort' roles such as leaf-cushions on wet ground, and

in local courtship gambits such as bending small shrubs on the ground (20, 21). Other diverse items include forms of food processing without tools, ways of dispatching ecto-parasites located during grooming, and grooming customs like the 'hand-clasp' that shows variant forms even in neighboring communities (73).

The orangutan list of 2003 (22) also includes a dozen different forms of tool use, several used for food extraction, such as holding a small stick in the mouth to extract seeds from *Neesia* fruits, or 'leaf-gloves' to handle spiky fruit. Hygiene/comfort examples include using a leaf napkin to wipe off sticky latex. The list as a whole is diverse, incorporating forms of arboreal locomotion, vocal sounds (some modified using leaves), variant nest constructions such as adding sun covers, and whether slow lorises are eaten or not, irrespective of availability.

The recent gorilla list of putative cultural variants (23) also displays diversity that includes making bridges across water, rubbing fruit to clean it or remove spines, incorporating tree-slapping into displays, using teeth as a 'fifth limb' in climbing, forms of bodily contact while travelling together, and forms of social play.

The Extent of Vertical Inter-generational Transmission. A detailed study of the foraging behavior of young wild orangutans before and after weaning concluded that their "diets were essentially identical to their mothers' even though not all mothers had the same diet" … "immatures selectively observed their mothers during extractive foraging, which increased goal-directed practice but not general manipulation of similar objects, suggesting observational forms of learning of complex skills" (40, p. 62). This conclusion was reinforced by a later study focused on 'peering' (39), referred to earlier. Over 2-4 years of age, infants foraged with their mother over 90% of the time; 94% of their feeding time was when the mother was also feeding, and 96% of their feeding was on the same items (39). The extent of co-feeding is clearly massive in pre-weaning years and likely to engender vertical social transmission of dietary profiles.

Years of mother-offspring association and co-feeding are typical of all the great apes and appears to lay down dietary preferences that change relatively little after weaning. Although the social learning implied may be as simple as enhancement of a food type by the mother feeding on it, such effects are likely to be profoundly important because large diet-sets need to be mastered, and selected from the yet more vast options

a tropical forest offers. This includes avoiding the numerous plant parts that are toxic, selecting relatively nutritious options and avoiding relatively poor ones. Chimpanzees may eat over 300 different food types (species x parts) in a year (74), and in the Lopé Park of Gabon, for example, fruit alone is taken from 114 different plants (75), selected from among many hundreds of potential food types available. The diet of gorillas may be similarly diverse, with gorillas in the Alfi mountains of Cameroon eating over 200 different food types, including fruits, seeds, leaves, stems, pith, flowers, bark, roots and invertebrates (75); and for the orangutans of Tanjung Putting in Borneo, the figure is again over 300 different food types (76). Yet the dietary profile of different populations may vary much, as suggested by earlier chimpanzee studies (77) and more recently confirmed even for neighbouring orangutan populations separated by a large river, that displayed 60% difference in diet, contrasting with intra-population homogeneity (78). Years of close apprenticeship to a mother who daily displays her knowledge of such a large yet selective diet-set likely offers an important means of achieving an adaptive response to this challenging complexity.

Time Depth of Cultural Transmission. Long-term field sites have shown that techniques such as termite fishing continue across several generations during the half-century of research now achieved. However this pales in comparison to the discoveries of real archaeological excavation, which in the Tai Forest of Ivory Coast reached a depth corresponding to 4,300 years, where remains of nut-cracking were identified (illustrated in figure 1 of reference (1)) beneath those currently generated on the surface by chimpanzees (79). Of course, this behavior may be very much older. Once such a beneficial technology becomes customary, it may continue in perpetuity pending major ecological perturbation. This example suggests that ape cultural inheritance spans not only the breadth of behavioral repertoires outlined earlier, but also a potentially significant time depth comparable to that familiar in organic evolution via genetic inheritance.

Does Ape Culture Instantiate A ‘New’ Form of Evolution?

Ape culture may have pervasive effects in shaping the behavioral repertoires of successive generations in the ways reviewed above, but does this imply an 'extension of biology' in the sense of instantiating a new form of evolution based not on genetic, but on social inheritance? This is what Dawkins proposed in his concept of culturally replicated 'memes' as analogies of genes, creating a new form of evolution in the case of human culture (80). The idea of aspects of culture such as language evolving through variation, (cultural) inheritance and selection goes back to Darwin's own writings (81) and was highlighted as the tenth and latest 'major evolutionary transition' of those proposed by Maynard-Smith and Szathmary (82). Mesoudi et al. (13) tackled the issue in finding abundant evidence for counterparts in human culture of eight major principles Darwin set out in the *Origin* (12): variation, selection, inheritance, adaptation, accumulation of modifications, geographic variation, convergence and changes of function. How do apes compare?

In addressing this we must be clear about what phenomena we are querying the potential 'evolution' of. If a chimpanzee invents a better hammer for nut-cracking (perhaps using a stone rather than wood), this may enhance that individual's biological fitness, with its genes better represented in future generations. That is natural selection, shaping biological evolution. However if others *copy* use of the new tool, the fitness (reproductive success) of that *cultural entity* – stone-tool use – will be enhanced through its spread, and to this extent we have *cultural evolution* of this *behavior*. It is this second phenomenon we are addressing here. Effects on individual culture-bearer's biological, inclusive fitness are a different matter and are returned to in a later section further below. We can now consider the eight evolutionary principles noted above.

Variation, Selection and Inheritance. These three principles can together be regarded as the core 'trinity' of Darwinian evolution. Their joint working is an 'evolutionary algorithm' that has been suggested to have the power to explain a multitude of phenomena beyond the living systems Darwin showed it applied to (83, 84).

As we have seen above, there is plentiful evidence in the great apes for the feature of *inheritance*, through social learning that provides sufficient fidelity to sustain traditions. There is also cultural *variation*, in part because compared to gene replication, social learning is prone to imperfect copying. In the arrays of cultural variants among

great apes discussed earlier in this article, there are plenty of behaviors that are displayed by many individuals in a community but not all (classed as 'habitual', rather than 'customary').

By contrast there seems yet to be little direct recording of cultural evolutionary *change* through *competition* and *selection* within this variation. This is perhaps unsurprising. During the human Stone Age, even when sophisticated, bilaterally-symmetric Acheulian blades showed an advance over earlier crude Oldowan tools, they changed relatively little over a million years (85). If such stability not implausibly characterizes chimpanzee nut-cracking and other cultural variants of apes, then we will see little evidence of cultural selection in human lifetimes. Of course, organic evolutionary change is itself often slow compared to scientific lifetimes; and instructive exceptions have often followed human-caused environmental perturbations that create new selection pressures. The classic example is of selection favoring dark morphs of peppered moths, better camouflaged against the sooty surfaces of the industrial revolution, then flipping to favor light colored morphs as the world became cleaner again.

Accordingly I have suggested that similar contexts of anthropogenic change may be fruitful for investigating cultural evolution in animals (1). Scientific experiments may offer a convenient instance. For example, in a pioneering cultural diffusion study, three juvenile chimpanzees were confronted with and avoided two novel objects (86). One youngster was then replaced with a naïve one, and this repeated, so after every third such cycle the triplet contained different individuals than earlier. Nevertheless, approaches to the objects steadily increased and in later 'generations' became customary (Supplementary Fig. S2). Accordingly, here there was *variation* in boldness, *inheritance* by naïve youngsters learning from bolder ones that the objects could be safely approached and explored, and competitive *selection* favoring small progressive steps in boldness. Playing with the objects could thus evolve as the norm in later generations, composed of different youngsters than the original shy ones. In a counterpart from the wild, two individuals from a human-habituated community of wild chimpanzees immigrated into a neighboring community that scientists were beginning to habituate, at which point habituation accelerated significantly (43).

In these examples an initially common variant (caution) was replaced competitively by another (boldness) which was adaptively superior (fear was unnecessary in these contexts). Likewise, in all the cultural diffusion experiments with apes cited earlier, improved foraging techniques spread across test groups to replace the less competitive behavioral state characterized by their absence. Here again there was thus *variation* (although in this case, experimenter-engineered), *inheritance* via social learning, and *competitive selection* favoring the cultural spread of the new foraging technique.

I suggest such experiments (as in 86) may thus allow us to explore the capacity of apes to exemplify, even if in a limited way, the operation of the 'Darwinian trinity' algorithm in a cultural context. Presumably all the cases of clearly beneficial cultural variants in the wild, like nut-cracking and other tool use, once did not exist; so where they are customary this is likely to have arisen through the operation of this algorithm.

Adaptation. The growth of boldness in the studies above (43, 86) indicate culturally evolved instances of *adaptation*, although adaptive payoffs were likely only mild. In the wild there is evidence that a more crucial level of adaptiveness has been delivered. Chimpanzees in Bossou, Guinea, were shown to be reliant on two forms of technology in particular, nut-cracking and pestle-pounding (a means of extracting nutritious pulp from the apex of palm trees), during the dry season when fruit became scarce (87), such that it is these cultural variants that allow these apes to inhabit otherwise inadequate habitats. How often culturally inherited technology is this critical remains difficult to judge at present, but many forms of tool use allow chimpanzees and orangutans to gain foodstuffs otherwise unavailable.

Such adaptations concern the local physical environment. Others may be societal. In a community of chimpanzees that customarily practice hand-clasp grooming, it may be adaptive to learn this from those already using it; and where a particular courtship gambit such as leaf-clipping has become common, it will likely be beneficial to adopt this as an action already recognized by one's potential mating partner.

Accumulation of Modifications. Human cultural modifications accumulate in an elaborate fashion that has no match in other animals, and display the most striking analogies with the richness of the evolved forms of the living world (9, 10, 13, 16, 83,

84). Many authors assert that we are the only species to exhibit cumulative culture (8, 9, 49, 56), but I suggest this may be premature. For example, chimpanzees in Goualougo use a stout stick to make a deep tunnel to subterranean termite nests and then use long stems to fish down the tunnels, first creating a distinct brush tip effective for fishing by stripping the stem ends through their teeth (72). They do this in a context where what to do is highly opaque, so it is difficult to see how it could have developed other than by a series of cumulative steps beginning with the more transparent context of fishing near the surface. Boesch (47) describes several other candidates for cumulative cultural evolution in chimpanzees. Direct evidence on the origins of such routines are lost in the past, but their complexity suggests elementary forms of cumulative culture, comparable perhaps to the achingly slow forms that characterized the early hominin Stone Age.

Geographic Variation. As the Darwinian algorithm operates in different regions, so organic characteristics differentiate and speciation may occur. Parallel effects occur in human cultural evolution (13, 88). As we have seen, great apes show evidence of different traditions at geographically-separated locations, and there is evidence from all the great ape genera that differences in putative cultural profiles are correlated with the geographic separation of communities (23, 24). As humans or other apes disperse over greater distances, one would expect both genetic and cultural similarities to diminish, and indeed Langergraber et al. (89) showed that cultural variation in chimpanzees is also correlated with genetic variation (but this does not mean genes explain the behavioural differences: see supplementary information to ref. 79 for further discussion of this study). Kamilar and Atkinson (90) demonstrated a nested structure in four samples of human cultural repertoires in N. America and New Guinea, which would occur if, as people disperse, traits are sequentially added in or lost. Consistent with earlier cladistic analyses of the branching pattern of chimpanzee profiles (91), chimpanzees were also found to display this pattern of nestedness across African sites. Orangutans did not, consistent with an earlier detailed orangutan study (27) and possibly reflecting a greater preponderance of vertical, mother-to-offspring transmission than horizontal transmission between communities.

Convergent Evolution. The Darwinian algorithm delivers some similar organic evolutionary outcomes in different places, despite different foundations. Cultural convergences of this kind appear to occur at different layers of relatedness amongst apes. An example within the same species is hand-clasp grooming, which has emerged and spread in some chimpanzee communities in the wild, but not others (20, 21, 73) as well as in an African sanctuary (35) and in groups in the USA (37). This is not simply individual invention because within-group spread of the behavior has been documented, indicating social transmission. Other convergences span different ape genera, such as use of fly swats and leaf napkins by both chimpanzees and orangutans; and again these are neither species instincts nor individually learned, because they are habitual at some locations yet absent at others, in the same species. Finally there are convergences between apes and other primates, as in the case of using stones as hammers to break open hard-cased food by distantly related long-tailed macaques (92) and capuchins (3, 93).

Change of Function. This is perhaps the category where we are most limited by lack of historical records. In humans, historical records suggest that just as morphology can evolve to serve a new function (arms becoming wings, for example), cultural elements may evolve new functions different to their original one (10). A candidate in great apes is that in chimpanzees, 'leaf-clip' (noisily shredding leaves with one's teeth) is reported as a courtship bid in some communities but used for other functions such as play in others (47) suggesting some of these alternatives may have evolved from each other or from a common ancestral function. However, it may yet be that the lack of evidence in this category is explained by that concerning limited cultural cumulation, noted above.

Culture extends Biology into New Realms of Evolution

The above focuses on how cultural evolution may match the 'template' for genetically-based Darwinian evolution, but cultural transmission by social learning also extends the scope of biological systems by incorporating additional dimensions of inheritance and evolution. Some of these have long been recognized in the literature concerning human cultural evolution, including the fact that in addition to intergenerational transmission

shared with genetic inheritance, cultural transmission can be horizontal (within or between groups, and extending to non-kin), or oblique, with learning from non-relatives in the prior generation (15). Above I have reviewed some of the evidence for learning from parents, typically the mother, in apes (38-41, 45). Horizontal and oblique transmission are commonly demonstrated in diffusion experiments (63-69), as well as in observational studies in the wild (42-44) and in sanctuaries (34). This makes cultural learning a powerful adaptive process, as does the fact that because it hinges on neural rather than genetic changes, it can act very much faster; some important things can even be learned observationally in a matter of minutes (94), even though complex skills may require a more extended observational apprenticeship (32, 39).

Additionally, whilst adaptive information is inherited genetically in a package at conception (even if activation is later adaptively contingent on environmental inputs), that which feeds into social learning can be temporally distributed, in at least two major ways. First, cultural transmission can be Lamarckian-like, with adaptive features acquired through one individual's lifetime passed on to those who learn from them. Second, a learner can progessively build up complex skills such as some forms of ape tool use, by repeated cycling through a process of observe, practice, observe again and practice again. This can be thought of as a spiral or helical process of learning in which cycles of observation and practice allow the learner to assimilate more in later observations than was possible in the earlier, more naïve stages (32, 39) (Fig. 3).

< insert Fig. 3 about here >

Social learning may also be selective in the assimilation of information, variously referred to as directed social learning (95), biased transmission (15) or social learning strategies (96), which can in principle shape adaptation and consequent evolutionary change, with no clear counterparts in the gene-based processes.

Selectivity in social learning. Evidence has been adduced for a number of the potential learning rules these analyses highlight, in great apes (97). Evidence for a 'copy the majority' rule, suggested by apparent conformity of chimpanzees in diffusion experiments (68), came in further experiments showing that both children and

chimpanzees would copy the choices of three other conspecifics rather than a single individual repeating the same act three times (98). Orangutans did not do this (98), possibly reflecting their less community-based social life. Evidence for discriminating more successful or productive options and copying these came from further experiments with chimpanzees (99). It has been suggested that preferentially copying individuals of high rank could serve this function too, and two studies have shown chimpanzees preferring to copy a high ranked over a lower ranked individual (100, 101). Finally, a tendency to learn from kin is shown by the studies of peering reviewed earlier, which showed extensive learning from the mother during apes' extended pre-weaning period (39, 41). After weaning, this widened to include peering at the activities of others, a plausibly adaptive shift from initially learning basic information from parents, then later targeting others to learn more specific skills, a trend identified in studies of human children, both observational (102) and experimental (103, 104). However, we still have only limited understanding of when and why an ape opts to learn socially, or not: for example, what determines when immigrants will either conform to local norms (30), or instead transmit their habitual skills to others (44)?

Interactions between genetic and cultural modes of inheritance and evolution

At the broadest level, culture extends biology insofar as some culturally transmitted behaviors are evolutionarily consequential; they have implications for practitioners' survival, reproduction and ultimate inclusive fitness (as opposed to the reproductive success of the cultural items themselves, discussed earlier). This may be less so for some cultural variants that appear relatively frivolous, such as staring at one's reflection in water in gorillas (23) or applying an autoerotic tool in orangutans (22), but varied forms of tool use by orangutans and chimpanzees appear highly functional in gaining access to rich resources like insect prey, nut kernels and honey. Indeed, some of these appear vital for chimpanzees to exploit niches that would otherwise exclude them (87). Other culturally transmitted behaviors play functional roles in grooming, social interactions and sexual courtship.

Another sense in which culturally transmitted behaviors may have been evolutionary important concerns their effects on organic evolution. Cetacean researchers

have proposed that cultural differentiation among whales has led to genetic differences (7, 105). For example, killer whales display 'eco-types' that specialize in hunting alternative prey such as seals or fish using very different techniques, and different clans exhibit other behavioral differences in their songs and migratory/resident patterns, despite often being sympatric (6, 7, 105, 106). Such effects are suggested to have driven other morphological and genetic differentiation, ultimately leading to incipient speciation, for it becomes difficult for a member of one culture to enter another and successfully manage the different foraging and courtship requirements there. This would be an instance of 'behavioral drive' (107-109), in which plasticity in behavior allows a species to exploit or create a new niche – in this case a culturally dependent one (e.g. fish versus seal hunting - hence 'cultural drive'). This in turn may create selection pressures acting on organic evolution, with effects such as the evolution of more robust jaws in the seal-hunters (6). Parallel hypotheses have been developed in the case of birdsong dialects driving speciation (110-111).

Such dramatically different specialisms as in killer whales is not apparent amongst great apes, although the extent to which there are similar processes at work in contrasts between, say, nut-cracking communities of chimpanzees, and the nearest neighbors that do not crack, would repay attention. However, one principal effect of complex culture on organic evolution in apes has been proposed, concerning encephalization and the cognitive sophistication it can provide: the Cultural Intelligence Hypothesis.

The Cultural Intelligence Hypothesis. In accord with a previously advanced Social (or 'Machiavellian') Intelligence hypothesis, relative brain size in different primate species was found to be predicted by the typical size of their social group and the concomitant demands on social cognition (59, 112). Great apes do not fit this pattern, showing high relative and absolute brain sizes, yet in the case of gorillas and orangutans, not living in large communities. However as all appear to display relatively complex cultures, the Cultural Intelligence Hypothesis suggests this complexity has selected for encephalization, either in a 'culture first' or an entwined culture-gene-brain co-evolution scenario (112-115). One side of this proposition may be glossed as 'culture makes you smart' - self-evident in the human case (9), insofar as present-day humans are smarter than a century earlier by virtue of the cumulative cultural achievements

from which they benefit. On a more modest scale, the same is proposed for the cultural endowment of great apes. The converse side of the proposal is that there is selection on the socio-cognitive capacities necessary to assimilate and store all the potential cultural repertoire available. In turn, it has been suggested that there will be correlated selection on technical and general intelligence, so as to benefit from the cultural input, as in intelligent tool-use, for example (114). One test of such ideas recently offered showed that when tested on the 'level playing field' of Zoo contexts, Sumatran orangutans scored higher on general intelligence than their Bornean cousins, as predicted by the more elaborate cultural repertoires of the Sumatran populations in the wild; moreover Sumatrans have 2-10% larger brain sizes (116).

Summary and Conclusions

Research particularly in the last two decades or so have shown that a 'second inheritance system' of social learning is widespread amongst animals, extending to all main classes of vertebrate and insects too (1, 2). Apes merit a special focus insofar as they have been subjected to an unmatched diversity and volume of observational and experimental studies by multiple research teams, which has revealed what appear to be the richest non-human cultural repertoires identified to date (although some cetaceans may show greater cultural *differentiation*, like the killer whales). This article has attempted to indicate the scope of ape culture research and the key points of its discoveries, particularly with respect to the theme of the present issue: how these cultural phenomena may extend biology, and its core evolutionary theory in particular. I have argued that the evidence supports the conclusion that the nature of social learning and its consequences in cultural transmission create new forms of evolution, that echo well established core principles of organic evolution, but also go beyond them in a number of fundamental ways, such as horizontal transmission and inheritance of acquired characteristics, thereby extending the scope of evolutionary processes we must now entertain. Moreover the primary genetically based forms of evolution shaped, and are also shaped by, the consequences of this second inheritance system, in complex ways we are only now starting to uncover.

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1. Whiten A (2017) A second inheritance system: the extension of biology through culture. *Interface Focus,* in press.
2. Whiten A, Ayala F, Feldman M, Laland KL (2017) The extension of biology through culture. Proc Natl Acad Sci USA this issue.
3. Fragaszy D, Others (2017) Extending attention: Young bearded capuchin monkeys practice percussive components of tool use in temporal synchrony with adults. *Proc Natl Acad Sci USA* this issue.
4. Perry S, Barrett BJ, Godoy I (2017) Older, sociable white-faced capuchins (*Cebus capucinus*) invent more social behaviors; younger monkeys innovate more in other contexts. *Proc Natl Acad Sci* USA this issue.
5. Hohmann G, Fruth B (2003) Culture in bonobos? Between species and within species behavior. *Curr Anthropol* 44:563-570.
6. Whitehead H, Rendell L (2015) *The Cultural Lives of Whales and Dolphins* (Chicago University Press, Chicago).
7. Whitehead H (2017) Gene-culture coevolution in whales and dolphins. *Proc Natl Acad Sci USA* this issue.
8. Pagel M (2012) *Wired For Culture: The Natural History of Human Communication* (Allen Lang, London).
9. Henrich J (2015) *The Secret of Our Success: How Culture is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter* (Princeton University Press, Princeton NJ).
10. Creanza N, Kolodny O, Feldman MW (2017) Cultural evolutionary theory: how culture evolves and why it matters. *Proc Natl Acad Sci USA* this issue.
11. Legare C (2017) The ontogeny of cumulative culture. *Proc Natl Acad Sci USA* this issue.
12. Darwin CD (1859) *On the Origin in Species by Natural Selection* (Murray, London)
13. Mesoudi A, Whiten A, Laland KN. (2004) Is human cultural evolution Darwinian? Evidence reviewed from the perspective of 'The Origin of Species'. *Evolution* 58:1-11.
14. Whiten A. (2005) The second inheritance system of chimpanzees and humans. *Nature* 437:52-55.
15. Boyd R, Richerson P (1985) *Culture and the Evolutionary Process* (University of Chicago Press, Chicago).

16. Mesoudi A (2017) Pursuing Darwin's curious parallel: Prospects for science of cultural evolution. *Proc Natl Acad Sci USA* this issue.
17. Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior* (Harvard University Press, Boston MA).
18. McGrew WC (1992) *Chimpanzee Material Culture: Implications for Human Evolution* (Cambridge University Press, Cambridge).
19. Boesch C, Tomasello M (1998) Chimpanzee and human cultures. *Curr Anthropol* 39:591- 694.
20. Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C 1999 Cultures in chimpanzees. *Nature* 399:682-685.
21. Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, et al (2001) Charting cultural variation in chimpanzees. *Behaviour* 138:1489-1525.
22. van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami, SS, Merrill, M (2003) Orangutan cultures and the evolution of material culture. *Science* 299:102-105.
23. Robbins MM, Ando C, Fawcett KA, Gruiter CC, Hedwig D, Iwata Y, Lodwick JL, Masi S, Salmi R, Stoinski TS et al (2016) Behavioural variation in gorillas: evidence of potential cultural traits. *PLOS ONE* 11:e0160483.
24. Whiten A (2012) Social learning, traditions and culture. *The Evolution of Primate Societies*, ed Mitani J, Call J, Kappeler P, Palombit R, Silk J (Chicago University Press, Chicago) pp 681-699.
25. van Schaik CP, Ancrenaz M, Djojoasmoro R, Knott CD, Morrogh-Bernard HC, Nuzuar KO, Atmoko SSU, van Noordwijk MA (2009) Orangutan cultures re-visited. *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*, ed Wich SA, Atmoko SSU, Setia TM, van Schaik CP (Oxford University Press, Oxford) pp 299-309.
26. Laland KN, Janik VM (2005) The animal cultures debate. *Tr Ecol Evol* 21:542-547.
27. Krützen M, Willems EP, van Schaik CP (2011) Culture and geographic variation in orangutan behavior. *Curr Biol* 21:1808-1812.
28. Shöning C, Humle T, Möbius Y, McGrew WC (2008) The nature of culture: technological variation in chimpanzee predation on army ants revisited. *J Hum Evol* 55:48-59.
29. Möbius Y, Boesch C, Koops K, Matsuzawa T, Humle T (2008) Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Anim Behav* 76:37-45.
30. Luncz LV, Boesch C (2014) Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behaviour despite frequent immigration of adult females. *Am J Primatol* 76:649–657.
31. Marshall-Pescini S, Whiten A (2008) Social learning of nut-cracking behaviour in East African sanctuary-living chimpanzees (*Pan troglodytes schweinfurthii*). *J Comp Psychol* 122: 186-194.

32. Whiten A 2015 Experimental studies illuminate the cultural transmission of percussive technology in *Homo* and *Pan*. *Phil Trans R Soc B* 370:20140359.
33. Santorelli CJ, Schaffner CM, Campbell CJ, Notman H, Pavelka MS, Weghorst JA et al. (2011) Traditions in wild spider monkeys are biased towards the social domain. *PLOS ONE* 6: e16863.
34. van Leeuwen EJC, Cronin KA, Haun SBM (2014) A group specific arbitrary tradition in chimpanzees. *Anim Cogn* 17:1421-1425.
35. van Leeuwen EJC, Cronin KA, Haun SBM, Mundry R, Bodamer MD (2012) Neighbouring chimpanzee communities show different preferences for social grooming. *Proc R Soc Lond B* 279:4362-4367.
36. Rawlings B, Davila-Ross M, Boysen ST (2014) Semi-wild chimpanzees open hard-shelled fruits differently across communities. *Anim Cogn* 17:891-899
37. Bonnie KE, de Waal FBM (2006) Affiliation promotes the transmission of a social custom: hand-clasp grooming among captive chimpanzees. *Primates* 47:27-34.
38. Lonsdorf EV, Pusey EA, Eberly L (2004) Sex differences in learning in chimpanzees. *Nature* 428:715-716.
39. Schuppli C, Meulman EJM, Forss SIM, Aprilinayati F, van Noordwijk MA, van Schaik CP (2016) Observational learning and socially induced practice of routine skills in immature orangutans. *Anim Behav* 119: 87-98.
40. Jaeggi AV, Dunkel LP, van Noordwijk MA, Wich SA, Sura AAL, van Schaik CP (2010) Social learng of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *Am J Primatol* 72:62-71.
41. Jaeggi AV, van Noordwijk MA, van Schaik CP (2008) Begging for information: mother-offspring food-sharing among wild Bornean orangutans. *Am J Primatol* 70:533-541.
42. Hobaiter C, Poiset T, Zuberbuhler K, Hoppitt W, Gruber T (2014) Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLOS Biology* 12:e1001960.
43. Samuni L, Mundry R, Terkel J, Zuberbuhler K, Hobaiter C. 2014 Socially learned habituation to human observers by wild chimpanzees. Anim Cogn 17:997-1005.
44. O'Malley RC, Wallauer W, Murray C, Goodall J (2012) The appearance and spread of ant fishing in the Kasekela chimpanzees of Gombe: A possible case of intercommunity cultural transmission. *Curr Anthropol* 53:650-670.
45. Musgrave S, Morgan D, Lonsdorf E, Mundry R, Sanz C (2016) Tool transfers are a form of teaching in chimpanzees. *Sci Rep* 6:34783.
46. Thornton A, McCauliffe K (2006) Teaching in wild meerkats. *Science* 313:227-229.

47. Boesch C (2012) *Wild Cultures: A Comparison Between Chimpanzee and Human Cultures.* (Cambridge University Press, Cambridge).
48. Haraiwa-Hasegawa M (1990) A note on the ontogeny of feeding. The Chimpanzees of the Mahale Mountains, ed Nishida T (University of Tokyo Press, Tokyo) pp 277-283.
49. Tomasello M, Call J, eds (1997). *Primate Cognition*. (Oxford University Press: Oxford).
50. Whiten A, Horner V, Litchfield CA Marshall-Pescini S (2004) How do apes ape? *Learn Behav* 32:36-52.
51. Galef BG, Whiten A. (2017) The comparative psychology of social learning. *APA Handbook of Comparative Psychology*. eds Call J, Burghardt G, Pepperberg I, Snowdon C, Zentall T (APA, Washington), In press.
52. Whiten A, Custance DM, Gomez J.-C, Teixidor P, Bard KA (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J Comp Psychol* 110:3-14.
53. Stoinski TS, Wrate JL, Ure N, Whiten A. (2001) Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *J Comp Psychol* 115:272-281.
54. Stoinski TS, Whiten A (2003) Social learning by orangutans in a simulated food-processing task. *J Comp Psychol*117:272-282.
55. Whiten A, McGuigan H, Hopper LM, Marshall-Pescini S. (2009) Imitation, over-imitation, emulation and the scope of culture for child and chimpanzee. *Phil Trans R Soc B* 364:2417-28.
56. Tennie C, Call J, Tomasello M (2009) Ratchetting up the ratchet: on the evolution of cumulative culture. *Phil Tran. R Soc B* 364 2405-2415...
57. Subiaul F (2015) What's special about human imitation? A comparison with enculturated apes. *Behav Sci* 6,13, doi:10.3390/bs6030013.
58. Whiten A (2017). Social learning and culture in child and chimpanzee. Ann Rev Psychol in press.
59. Whiten A, van de Waal E (2017) Social learning, culture and the 'socio-cultural brain' of human and non-human primates. Neurosci Biobehav Rev in press.
60. Carvalho S, McGrew W. (2010) The origins of the Oldowan: why chimpanzees are still good models for technological evolution in Africa. *Stone Tools and Fossil Bones,* ed Domínguez-Rodrigo M (Cambridge University Press, Cambridge), pp 201-221.
61. Boesch C, Marchesi P, Marchesi N, Fruth B, Joulian F (1994) Is nutcracking in wild chimpanzees a cultural behaviour? *J Hum Evol* 26:325-338.
62. McGrew WC, Ham RM, White LJT, Tutin CEG, Fernandez M (1997) Why don't chimpanzees in Gabon crack nuts? *Int J Primatol* 18:353-374.
63. Whiten A, Mesoudi A (2008) Establishing an experimental science of culture: animal social diffusion experiments. *Phil Trans R Soc B* 363:3477-3488.

64. Whiten A, Caldwell CA, Mesoudi A (2016) Cultural diffusion in humans and other animals. *Curr Op Psychol* 8:15-21.
65. Horner V, Whiten A, Flynn E de Waal FBM (2006) Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proc Natl Acad Sci USA* 103:13878-13883.
66. Dindo M, Stoinski T, Whiten A (2011) Observational learning along cultural transmission chains in orangutans. *Biol Lett* 7:181-183.
67. Whiten A, Horner V, de Waal FBM (2005) Conformity to cultural norms of tool use in chimpanzees. *Nature* 437:737-740.
68. Bonnie KE, Horner V, Whiten A, de Waal FBM (2007) Spread of arbitrary customs among chimpanzees: a controlled experiment. *Proc R Soc Lond B* 274:367-372.
69. Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth S P, Schapiro SJ, de Waal FBM (2007) Transmission of multiple traditions within and between chimpanzee groups. *Curr Biol* 17:1038-1043.
70. Pruetz JD, Bertolani P (2007) Savanna chimpanzees (Pan troglodytes verus) hunt with tools. *Curr Biol* 17: 412-417.
71. Pruetz JD, Bertolani P, Boyer Ontl K, Lindshield S, Shelley M, Wessling EG (2015) New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Senegal. *R Soc open sci* 2:140507.
72. Sanz C, Call J, Morgan D (2009) Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol Lett* 5:293-296.
73. Nakamura M, Uehara S (2004) Proximate factors of different types of grooming hand-clasp in Mahale chimpanzees: implications for chimpanzee social customs. *Curr Anthropol* 45:108-114.
74. Inskipp T (2005) Chimanzee (Pan troglodytes) *World Atlas of Great Apes and Their Conservation*, ed J Caldecott, L Miles (Univ California Press, Berkeley) pp 53-81.
75. Ferriss S (2005) Western gorilla (*Gorilla gorilla*) *World Atlas of Great Apes and Their Conservation*, ed J Caldecott, L Miles (Univ California Press, Berkeley) pp 105-127.
76. McConkey K (2005) Bornean orangutan (*Pongo pygmaeus*) World Atlas of Great Apes and Their Conservation, ed J Caldecott, L Miles (Univ California Press, Berkeley) pp 161-183.
77. Nishida T, Wrangham RW, Goodall J, Uehara S (1983) Local differences in plant feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *J Hum Evol* 12:467-480.
78. Bastian M, Zweifel N, Vogel ER, Wich SA, van Schaik CP (2010) Diet traditions in wild orangutans. *Am J Phys Anthropol* 143:175-187.

79. Mercader J, Barton H, Gillisepie J. et al (2007) 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proc Nat Acad Sci USA* 104:3043-3048.
80. Dawkins R (1976) *The Selfish Gene* (Oxford University Press, Oxford).
81. Darwin C. (1871) *The Descent of Man and Selection in Relation to Sex* (Murray, London).
82. Maynard-Smith J, Szathmary E (1995). *The major transitions in evolution* (Freeman, Oxford).
83. Dennett D (1995) *Darwin's Dangerous Idea* (Penguin, London).
84. Ridley M (2015) *The Evolution of Everything* (Fourth Estate, London.
85. Stout D (2011) Stone toolmaking and the evolution of human culture and cognition. *Phil Trans R Soc B* 366:1050-1059.
86. Menzel EW, Davonport RK, Rogers CM. (1972) Protocultural aspects of chimpanzees' responsiveness to novel objects. *Folia Primatol* 17:161-170.
87. Yamakoshi G 1998 Dietary responses to food scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *Am J Phys Anthropol* 106: 283-295.
88. Langergraber KE et al (2010) Genetic and cultural similarity in chimpanzees. *Proc R Soc B* 277:408-416.
89. Gray RD, Watts J (2017) Macro matters: Cultural macroevolution and the prospects for an evolutionary science of human history. *Proc Natl Acad Sci USA* this issue;.
90. Kamilar JM, Atkinson QD (2014) Cultural assemblages show nested structure in humans and chimpanzees but not orangutans. *Proc Natl Acad Sci USA* 111:111-115.
91. Lycett SJ, Collard M, McGrew WC (2009) Cladistic analyses of behavioural variation in wild Pan trodlodytes: exploring the chimpanzee culture hypothesis. J Hum Evol 57:337-349.
92. Gumert MD, Malaivijitnond S. (2012 Marine prey processed with stone tools by burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. Am J Phys Anthropol 149:447-457.
93. Fragaszy DM, Izar P, Visalberghi E, Ottoni EB, Oliveria MG (2004) Wild capuchin monkeys (*Cebus libidinosus*) use anvials and stone pounding tools. *Am J Primatol* 64:359-366.
94. Whiten A (1998) Imitation of the sequential structure of actions by chimpanzees *(Pan troglodytes*). *J Comp Psychol* 112:270-281
95. Coussi-Korbel S,Fragaszy DM (1995) On the relation between social dynamics and social learning. *Anim Behav* 50:1441-1450.
96. Laland KN (2004) Social learning strategies. *Learn Behav* 32:4-14.
97. Price EE, Wood LA, Whiten A. (2017) Adaptive cultural transmission biases in children and nonhuman primates. *Inf Behav Dev* in press.
98. Haun DB, Rekers Y, Tomasello M (2012) Majority-biased transmission in chimpanzees and human children, but not orangutans. *Curr Biol 22*:727-731

786 99. Vale GL, Flynn EG, Lambeth SP, Schapiro SJ, Kendal RL (2011) Public information use in
787 chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *J Comp Psychol* 128:215-223.
788 100. Horner K, Proctor D, Bonnie KE, Whiten A, de Waal FBM (2010) Prestige affects cultural learning
789 in chimpanzees. *PLoS One* 5:e10625
790 101. Kendal RM, Hopper LM, Whiten A, Brosnan SF, Lambeth SP, Schapiro SJ, Hoppitt W (2015)
791 Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity.
792 *Evol Hum Behav* 36:65-72.
793 102. Henrich, J., & Broesch, J. (2011) On the nature of cultural transmission networks: evidence from
794 Fijian villages for adaptive learning biases. *Phil Trans R Soc B 36*6:1139–1148.
795 103. Harris PL, Corriveau KH (2011) Young children's selective trust in informants. *Phil Trans R Soc B*
796 366:1179–87.
797 104. Lucas AJ, Burdett ERR, Burgess V, Wood L, McGuigan N, Harris PL, Whiten A (2017) Children's
798 selective copying of their mother versus an expert. *Child Dev* in press
799 105. Carroll EL, Baker CS, Watson M, Alderman R, Bannister J, Gaggiotti OE, Cröcke DR, Pateneude
800 N, Harcourt R (2015) Cultural traditions across a migratory network shape the genetic structure of
801 southern right whales around Australia and New Zealand. *Sci Rep* 5:16182.
802 106. Foote AD, Vijay N, Avila-Arcos MC, Baird RW, Durban JW, Fumagalli M, Gibbs RA, Hanson MB,
803 Korneliussen TS et al (2016) Genome-culture co-evolution promotes rapid divergence of killer
804 whale ecotypes. *Nat.Comm* 7:11693.
805 107. Wyles JS, Kunkel JG, Wilson AC (1983) Birds, behavior and anatomical evolution. *Proc Natl*
806 *Acad Sci USA* 80:4394-4397.
807 108. Wilson AC (1985) The molecular basis of evolution. *Sci Amer* 253:148-157.
808 109. Bateson PPG (2004) The active role of behavior in evolution *Biol Philos* 19:283-298.
809 110. Grant BR, Grant PR (2002) Simulating secondary contact in allopatric speciation : an empirical
810 test of premating isolation. *Biol J Linn Soc* 76:545-556.
811 111. Grant PR, Grant BR. (2002) Adaptive radiation of Darwin's finches. *Am Sci* 90:130-139.
812 112. Whiten A, van Schaik CP (2007) The evolution of animal 'cultures' and social intelligence. *Phil.*
813 *Trans. Roy. Soc. B* 362: 603-620.
814 113. van Schaik CP, Burkart JM (2011) Social learning and evolution: the cultural intelligence
815 hypothesis. *Phil Trans R Soc B* 366:1179–87.
816 114. Burkart J, Schübiger MN, van Schaik CP (2017) The evolution of general intelligence *Behav*
817 *Brain Sci* in press.
818 115. Street SE, Navarette AF, Reader SM, Land KN (2017) Coevolution of cultural intelligence,
819 extended life history, sociality and brain size in primates. *Proc Natl Acad Sci USA* this issue.

116. Forss, SIF, Willems E, Call J, van Schaik CP (2016) Cognitive differences between orangutan species: a test of the cultural intelligence hypothesis. *Sci Rep* 6:30516.

824 Figure captions
825
826 Fig. 1. ‘Peering’ (ref. 39) in a juvenile orangutan as her mother extracts termites from
827 dead wood. Photo courtesy of Christiaan Conradie and Caroline Schuppli.
828
829 Fig. 2. Convergent evidence for a culture of nut-cracking in chimpanzees. Evidence for
830 nut-cracking at multiple sites in West Africa (20, 21, 60) (white stars) but absent at others
831 (black stars). Independent studies confirmed availability of raw materials at two such
832 sites (61, 62). Experiments showed East African chimpanzees did not initially nut-crack
833 (Phase 1), but half exposed to a proficient model began to do so (Phase 2) and all did
834 once all so exposed (Phase 3) (31,32).
835
836 Fig. 3. ‘Helical Curriculum’ model of skill development (after Ref. 32). Over repeated
837 cycles of observation-of-expert and practice, the social learner is able to assimilate more
838 information from the expert and gradually improve their skill level. See text for more
839 explanation.
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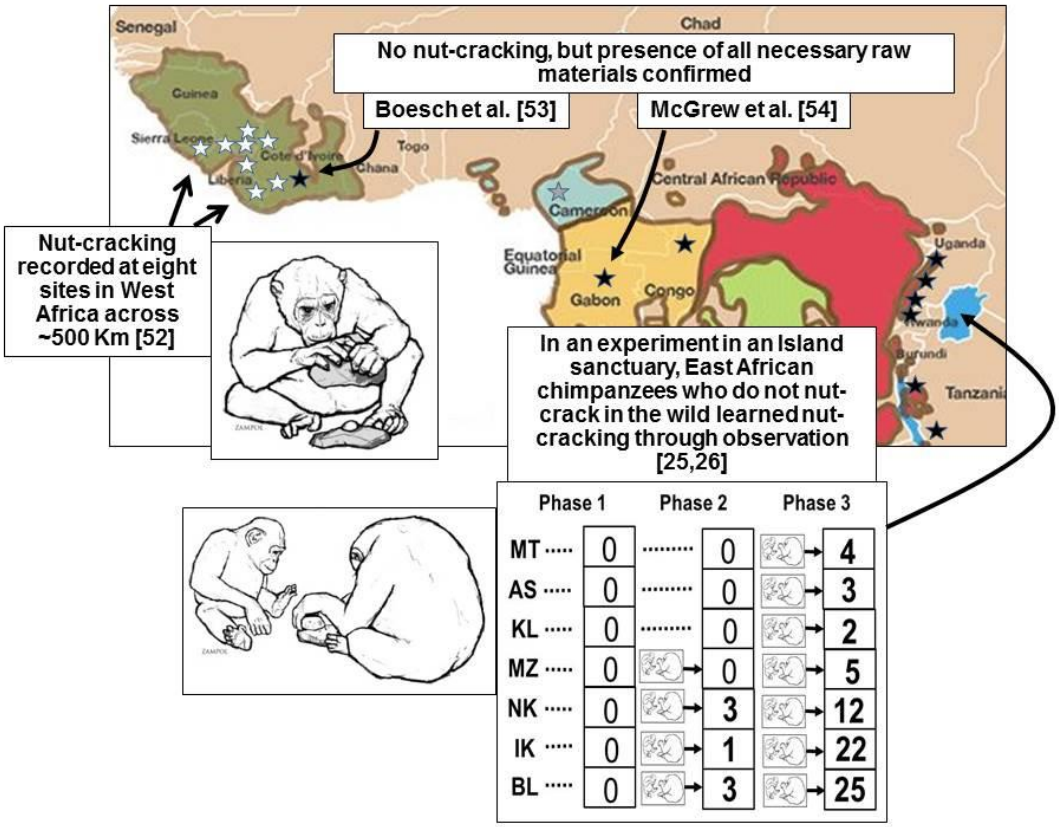
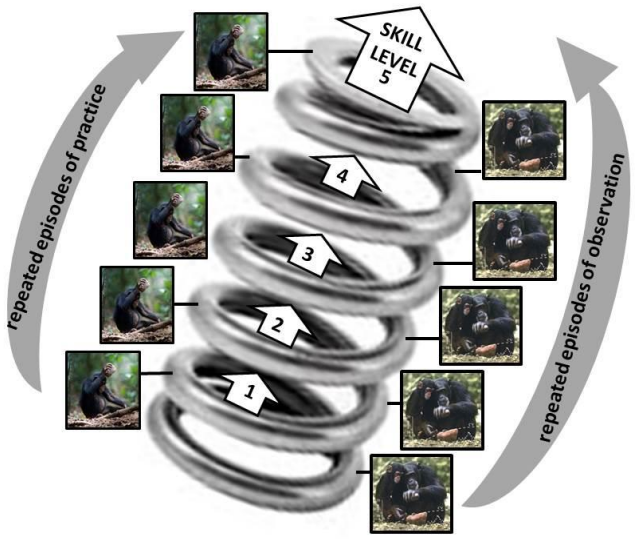

Senegal
Chad
No nut-cracking, but presence of all necessary raw materials confirmed
Boesch et al. [53]
McGrew et al. [54]
Guinea
Sierra Leone
Cote d'Ivoire
Liberia
Ghana
Togo
Central African Republic
Cameroon
Equatorial Guinea
Gabon
Congo
Uganda
Rwanda
Burundi
Tanzania
Nut-cracking recorded at eight sites in West Africa across ~500 Km [52]
In an experiment in an Island sanctuary, East African chimpanzees who do not nut-crack in the wild learned nut-cracking through observation [25,26]
Phase 1
Phase 2
Phase 3
MT ..... 0 ..... 0 → 4
AS ..... 0 ..... 0 → 3
KL ..... 0 ..... 0 → 2
MZ ..... 0 → 0 → 5
NK ..... 0 → 3 → 12
IK ..... 0 → 1 → 22
BL ..... 0 → 3 → 25

843


SKILL LEVEL 5
4
3
2
1
repeated episodes of practice
repeated episodes of observation

844